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### Parents influence asymmetric sibling competition: Experimental evidence with partially dependent young

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## PARENTS INFLUENCE ASYMMETRIC SIBLING COMPETITION: EXPERIMENTAL EVIDENCE WITH PARTIALLY DEPENDENT YOUNG

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**Abstract.** Asymmetric sibling competition, which occurs when some siblings hatch as stronger competitors than others, is an important component of avian reproductive strategies. Here, we report two experiments on the burying beetle *Nicrophorus vespilloides* investigating how parents might influence the outcome of asymmetric sibling competition. In this species, as in altricial birds, different-aged offspring compete for resources provided by the parents. However, unlike altricial birds, offspring depend only partially on their parents for resources, and parents adjust the brood size directly through filial cannibalism. In the first experiment, we compared the growth and survivorship of different-aged offspring when parents could and could not influence asymmetric sibling competition. In the second experiment, we recorded behavioral interactions between different-aged offspring and parents. We found that senior offspring (early-hatched) grew faster than juniors (late-hatched) when parents were present and could influence the outcome of sibling competition, whereas seniors and juniors grew at similar rates when parents were removed. Thus, seniors benefited more than did juniors when the offspring could obtain resources by begging from the female parent. There was no difference in the survivorship of seniors and juniors. We also found that seniors and juniors spent a similar amount of time feeding from female parents, but juniors spent more time begging and were less effective at begging than seniors. Interestingly, juniors spent more time begging only as long as seniors also begged, suggesting that juniors adjusted their begging effort in response to direct competition against seniors for resources provided by parents. Our study provides novel insights into the ecological significance of asymmetric sibling competition by showing that asymmetric sibling competition took place when parents were present and offspring could obtain resources by begging. In contrast, we found no evidence of asymmetric sibling competition when parents were absent and offspring obtained resources solely by self-feeding.

**Key words:** asynchronous hatching; begging; brood reduction; burying beetles; *Nicrophorus vespilloides*; parental care; partially dependent young; self-feeding; sibling rivalry.

### INTRODUCTION

Asymmetric sibling competition occurs whenever multiple offspring share a limited resource, such as a common source of food, and some offspring are born or hatch as stronger competitors than others (Parker et al. 1989, Mock and Parker 1997). For decades, ecologists have recognized asymmetric sibling competition as an important component of avian reproductive strategies (Lack 1968, Magrath 1990, Stoleson and Beissinger 1995, Mock and Parker 1997). In birds, the primary cause of asymmetric sibling competition is asynchronous hatching (Glassey and Forbes 2002), which occurs when parents start incubating the eggs before the clutch has been completed (Magrath 1990, Stoleson and Beissinger 1995). Lack (1968) suggested that asynchronous hatching allows parent birds to produce an optimistic initial

brood size that can be trimmed downward should the availability of resources be poor. According to Lack, the resulting competitive asymmetries based on hatching order provide parents with an indirect and low-cost mechanism for brood reduction. Although the adaptive value of asynchronous hatching is controversial due to a number of competing hypotheses, the effects of asynchronous hatching on sibling competition are well documented (Magrath 1990, Stoleson and Beissinger 1995, Mock and Parker 1997).

Asymmetric sibling competition caused by asynchronous hatching has recently attracted much interest because it influences the resolution of familial conflicts of interests over resource allocation (Mock and Parker 1997, Cotton et al. 1999, Glassey and Forbes 2002, Parker et al. 2002, Royle et al. 2002, Johnstone 2004). Theory predicts that stronger siblings will be under selection to bias the resolution of familial conflicts toward their own optimum by behaving selfishly toward weaker siblings (Parker et al. 1989). However, the ability of stronger siblings to do so would depend on how

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parental behaviors influence the outcome of sibling competition (Mock and Parker 1997, Krebs 2002). Parents of some birds, including herons, raptors, and songbirds, distribute resources passively based on the outcome of asymmetric sibling competition (Mock and Parker 1997), whereas parents of other birds, including some parrots, actively distribute resources evenly among different-aged siblings (Krebs 2002). Thus, evidence from studies on birds suggests that there is considerable interspecific variation in how parents influence the outcome of asymmetric sibling competition.

One way to improve our understanding of asymmetric sibling competition, and of how parents influence the outcome of asymmetric sibling competition, is to extend the current research program to non-avian species, for example, the burying beetle *Nicrophorus vespilloides*. This species breeds on small vertebrate carcasses, a limited resource shared by multiple offspring (Eggert and Müller 1997, Scott 1998). Sibling competition has important fitness consequences because offspring growth is negatively affected by the number of competitors in the brood (Bartlett 1987) and the amount of begging in the brood (Lock et al. 2004). Offspring growth, which occurs entirely while larvae stay on the carcass, determines adult body size (Bartlett and Ashworth 1988), which, in turn, influences survival (Lock et al. 2004) and success in competition for breeding opportunities (e.g., Müller et al. 1990). Sibling competition in *N. vespilloides* is of particular interest because siblings compete for resources partly by begging for predigested carrion from the parents and partly by self-feeding directly from the carcass (Smiseth and Moore 2002, Smiseth et al. 2003b). *N. vespilloides* offspring hatch asynchronously over a mean period of 30 hours (Smiseth et al. 2006), and asynchronous hatching may result in competitive asymmetries based on hatching order, as found in many altricial birds (Mock and Parker 1997).

In this study we used a novel experimental approach to investigate how parents may influence the outcome of asymmetric sibling competition in *N. vespilloides*. In our first experiment, we manipulated the parents' ability to influence sibling competition by removing parents experimentally from one-half of the broods, thereby forcing offspring to compete for resources by self-feeding directly from the carcass. In the remaining broods, where female parents were left to care for the offspring, offspring could compete for resources by begging for predigested carrion from the female parent. Thus, we tested whether the presence or absence of female parents had a differential effect on the growth and survivorship of senior (i.e., early-hatched) and junior (i.e., late-hatched) offspring. In our second experiment, we studied behavioral interactions between seniors and junior offspring and female parents at 24-hour intervals starting when seniors were 1 hour old and ending when juniors were 49 hours old. This experiment allowed us to test a difference in the begging behavior of,

and parental behavior toward, seniors and juniors across different age groups. We recorded the following three behaviors of seniors and juniors: (1) time spent feeding from parents, (2) time spent begging, and (3) effectiveness of begging (i.e., the return in parental resources for a given amount of begging). Taken together, these two experiments provide valuable insights into how parents influence the outcome of asymmetric sibling competition.

## MATERIALS AND METHODS

### *General procedures*

We used beetles from an outbred laboratory population (for details, see Smiseth et al. 2006). We placed pairs of non-sibling virgin female and male beetles in a transparent container ( $17 \times 12$  cm and 6 cm high) filled with 1 cm of moist peat and provided them with a previously frozen mouse carcass (supplied from Livefoods Direct Ltd, Sheffield, UK), the size of which was kept within a limited range (carcass mass  $24.9 \pm 2.3$  g and  $27.9 \pm 1.9$  g [mean  $\pm$  SD] for the first and second experiments, respectively). Two days after females started laying eggs, and before the eggs hatched, the female and the carcass were transferred to a new container filled with 1 cm of moist peat. The male was removed at this stage because males are less involved in provisioning of resources for the offspring than are females, and male assistance in provisioning of resources has no detectable effect on offspring growth or survival (Müller et al. 1998, Smiseth et al. 2005). The eggs were left to hatch in the old container, which was checked for the presence of newly hatched offspring four times a day.

*Nicrophorus vespilloides* offspring hatch asynchronously over a mean period of 30 h (Smiseth et al. 2006). As in altricial birds, different-aged offspring compete by begging for resources provided by the parents (Kilner and Johnstone 1997), and early-hatched siblings may be competitively superior to late-hatched ones because the former are older and larger (Magrath 1990, Mock and Parker 1997, Cotton et al. 1999). In both experiments, we established experimental broods comprising two groups of offspring that differed with respect to hatching order and size rank. Each group of offspring comprised 10 newly hatched offspring of mixed maternal origins. The first group, termed "seniors," was added 24 h before the last group, termed "juniors." This experimental treatment is well within the natural variation with respect to brood size ( $21 \pm 10$  offspring [mean  $\pm$  SD], range 2–47 offspring; Smiseth and Moore 2002) and asynchronous hatching in this species ( $30 \pm 10$  h [mean  $\pm$  SD], range 16–56 h; Smiseth et al. 2006). We provided females with broods only after their own eggs had started hatching, because females exhibit temporal kin recognition, killing offspring that arrive before their own eggs have started to hatch (Müller and Eggert 1990).

*Experiment 1: Competition in presence  
and absence of parents*

To compare growth and survivorship of different-aged offspring when female parents could and could not influence asymmetric sibling competition, we randomly removed female parents from 27 broods and left female parents in 23 broods. We monitored effects on growth by weighing seniors and juniors at 24-h ( $\pm 15$  min) intervals starting at the time of hatching and ending when offspring reached the age of 120 h (that is, the age at which offspring cease feeding and disperse from the carcass). To discriminate seniors from juniors, we marked offspring by cutting the outer part of either the right or the left hind leg when the offspring were 24 h of age, a treatment that has no effect on offspring fitness because adult legs are generated from imaginal discs that are unaffected by the cutting of legs in the larval stage (Rauter and Moore 2002). In one-half of the broods, we marked all seniors by cutting the right leg and all juniors by cutting the left leg, while in the other half of the broods, we marked all seniors by cutting the left leg and all juniors by cutting the right leg. At each 24-h interval, we separated the seniors or juniors based on leg marks, and noted the number of seniors and juniors in the brood and the total mass of all seniors and juniors. From these numbers, we calculated mean body mass for seniors and juniors in a given brood for a given age. We predicted that offspring would grow better in the presence of female parents than in their absence, given that theory predicts that parents should provide resources only if provisioning enhances offspring growth (Clutton-Brock 1991). We also expected that seniors would grow better than juniors, given that asynchronous hatching might establish competitive asymmetries within the brood. Finally, we tested whether the presence or absence of the female parent had a differential effect on the growth of seniors and juniors; that is, we tested for an effect of the interaction between the presence or absence of the female parent and offspring size rank. Although we cannot derive specific predictions for how the presence or absence of parents would affect the growth of seniors and juniors, such a test would provide novel insights into how parents might influence the outcome of asymmetric sibling competition.

We monitored offspring survivorship by counting the number of seniors and juniors in each brood that had survived to the age at which the offspring dispersed from the carcass. The age of dispersal is defined as the day at which the offspring left the crypt surrounding the carcass. Dispersal from the carcass is synchronous and occurred normally when the seniors were 144 h of age and the juniors were 120 h of age. For the analyses, we calculated the percentage of seniors and juniors in each brood that had survived until the age of dispersal. We predicted a main effect of the presence or absence of parents because theory predicts that parents provide care to enhance the survivorship of their offspring (Clutton-Brock 1991). We also tested for a main effect of

size rank on offspring survivorship, as well as for an effect of the interaction between the presence or absence of the female parent and offspring size rank. The last two tests were conducted to establish whether asymmetric sibling competition had lethal effects similar to those reported for herons and raptors (Mock and Parker 1997).

*Experiment 2: Behavioral interactions*

We conducted a second experiment on 22 broods to elucidate the behavioral interactions between seniors and juniors and female parents. In this experiment, we distinguished between seniors and juniors based on body size. Body size is a reliable method in this species, owing to the extremely rapid growth over the first few days after hatching (Smiseth et al. 2003b). Observations were conducted under photographic red light using instantaneous scan sampling every 1 min for 30 min in accordance with the protocol previously developed (Smiseth and Moore 2002, 2004, Smiseth et al. 2003b, 2005, Lock et al. 2004). At each scan, we counted the number of seniors and juniors in a given brood that were feeding from the parent and that were begging. An offspring was scored as feeding when there was mouth-to-mouth contact between it and the parent, and it was scored as begging when raising its head toward the parent while waving the legs or touching the parent (Rauter and Moore 1999). At each scan, we also recorded whether the female was in close proximity to the offspring, defined as a distance corresponding to less than the width of its pronotum from the nearest offspring. This distance corresponds to the distance from which offspring start begging (Rauter and Moore 1999). Observations were conducted at 24-h ( $\pm 15$  min) intervals starting 1 h after the seniors were placed on the carcass (to avoid disturbance) and ending when the juniors were 49 h of age. We did not observe behaviors of older offspring because offspring cease begging at 72 h of age (Smiseth et al. 2003b). Thus, all broods were observed four times: (1) when seniors were 1 h old, (2) when seniors were 25 h old and juniors were 1 h old, (3) when seniors were 49 h old and juniors were 25 h old, and (4) when juniors were 49 h old.

For each age, we calculated the mean time spent feeding from the female parents by seniors and juniors as  $p = (\Sigma m/L)(100/30)$ , where  $\Sigma m$  is the total number of resource-provisioning events involving either seniors or juniors during the 30-min observation period, and  $L$  is the number of seniors or juniors in the brood. We also calculated the average percentage of time spent begging by seniors and juniors as  $b = (\Sigma b/L)(100/p)$ , where  $\Sigma b$  is the total number of begging events by any of the seniors or juniors in a brood during an observation session,  $L$  is the number of seniors or juniors for a given brood, and  $p$  is the number of scans during which the female was near the larvae (Smiseth et al. 2003b). Finally, we calculated the average effectiveness of begging for seniors and juniors as  $m = (\Sigma m/\Sigma b)100$ , where  $\Sigma m$  and  $\Sigma b$  are as

TABLE 1. Full repeated-measures GLM model for effects of the presence or absence of female parents, offspring size rank (seniors vs. juniors), and age (0, 24, 48, 72, 96, and 120 h) on the body mass of burying beetle *Nicrophorus vespilloides* offspring.

Factor	<i>F</i>	df	<i>P</i>
Between-subjects			
Presence or absence of parents	240.14	1, 48	<0.001
Within-subjects			
Age	3056.6	2.85, 136.75	<0.001
Size rank	20.15	1, 48	<0.001
Size rank $\times$ presence or absence of parents	8.76	1, 48	0.005
Age $\times$ presence or absence of parents	93.15	2.85, 136.75	<0.001
Age $\times$ size rank	23.29	2.67, 127.91	<0.001
Age $\times$ presence or absence of parents $\times$ size rank	4.67	2.67, 127.91	0.006

Notes: Because our sole interest was to examine the effects of the presence or absence of female parents and size rank on offspring growth (i.e., the change in offspring body mass as a function of age), we focus on the final three terms of the model. We compare the body mass of seniors and juniors when they are of the same age.

previously defined. These are the same measures used in our previous studies of begging. Although effectiveness of begging overlaps with the other two parameters, we include this parameter because it provides valuable information on the competitive success of seniors and juniors that cannot be inferred from the other parameters.

We predicted that time spent feeding from parents and begging would change with age, increasing from the age of 1 h to the age of 25 h, and then decreasing from the age of 25 h to the age of 49 h, in accordance with previous studies on *N. vespilloides* and other species of burying beetles (Rauter and Moore 1999, Smiseth et al. 2003b). We expected that seniors would spend more time feeding from the parents, but that juniors would spend more time begging and would be less effective at begging than seniors, in accordance with studies on altricial birds (Price and Ydenberg 1995, Lotem 1998, Cotton et al. 1999). Finally, we tested whether seniors and juniors differed in how they changed their behaviors as they aged; that is, we tested for an effect of the interaction between offspring age and size rank. Although we cannot derive specific predictions for how the behavior of seniors and juniors would change with age, such tests provide valuable insights into the ontogeny of behavioral interactions between seniors and juniors and female parents.

#### Statistical analyses

We investigated how female parents influence the outcome of asymmetric sibling competition by testing for effects of the presence or absence of female parents and hatching order (i.e., seniors vs. juniors) on offspring body mass from the time of hatching and at 24-h intervals until the age of 120 h (Table 1). We used repeated-measures GLM with brood as subject to avoid pseudoreplication associated with using multiple measurements from each brood. We entered the presence or absence of female parents as a between-subjects factor with two levels: offspring size rank as a within-subjects factor with two levels (seniors and juniors), and

offspring age as a within-subjects factor with six levels (0, 24, 48, 72, 96, and 120 h). Our main aim was to address the effect of the interaction between the presence or absence of female parents and size rank on offspring growth, which in our model is the effect of offspring age on offspring body mass (Table 1).

We also used repeated-measures GLM to investigate effects on offspring survivorship. In this model, we entered the presence or absence of female parents as a between-subjects factor with two levels, while offspring size rank was entered as a within-subjects factor with two levels (seniors and juniors).

Finally, we used repeated-measures GLM to investigate behavioral interactions between seniors and juniors and their parents. In these models, we entered size rank as a within-subjects factor with two levels (seniors and juniors), and offspring age as a within-subjects factor with three levels (1, 25, and 49 h; Table 2).

All data were analyzed using SYSTAT 10 (SPSS, Chicago, Illinois, USA). For all tests, we report the Greenhouse-Geisser test statistic, which provides de-

TABLE 2. Repeated-measures GLMs testing for effects of offspring age (1, 25, and 49 h) and size rank (seniors vs. juniors) on three behaviors expressed in interactions between *Nicrophorus vespilloides* offspring and their parents.

Behavior and factor	<i>F</i>	df	<i>P</i>
Time spent feeding from parents			
Age	20.50	2, 42	<0.001
Size rank	0.29	1, 21	0.60
Age $\times$ size rank	0.50	2, 42	0.61
Time spent begging			
Age	17.79	2, 42	<0.001
Size rank	25.14	1, 21	<0.001
Age $\times$ size rank	3.94	2, 42	0.027
Effectiveness of begging			
Age	8.03	2, 42	0.001
Size rank	10.40	1, 21	0.005
Age $\times$ size rank	0.15	2, 42	0.86

Note: We compare the behavior of seniors and juniors when they are of the same age.

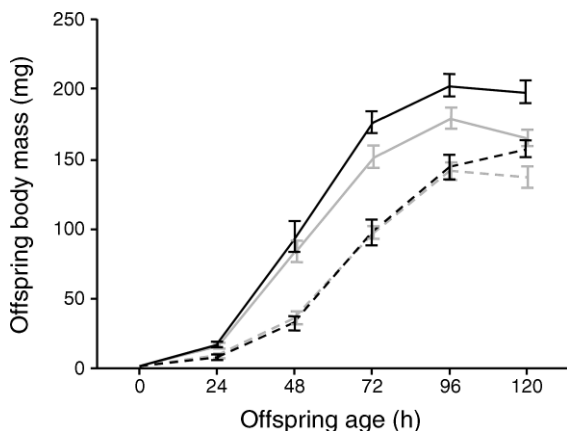


FIG. 1. Effects of the presence or absence of the female parent on the growth of senior (black lines) and junior (gray lines) burying beetle *Nicrophorus vespilloides* offspring from hatching and at consecutive 24-h intervals until 120 h of age. Data are presented as means  $\pm$  2 SE. Solid lines represent offspring body mass when parents were present, and dashed lines represent offspring body mass when parents were absent.

degrees of freedom that are not necessarily whole numbers. Data on offspring body mass and survivorship were normally distributed, while all behavioral parameters were arcsine square-root transformed to achieve a normal distribution (Zar 1984); two-tailed tests were used.

## RESULTS

### Experiment 1: Competition in presence and absence of parents

Offspring grew significantly better when female parents were present and the offspring could compete for resources by begging than when female parents were absent (Table 1, Fig. 1). Furthermore, seniors grew faster than juniors, as predicted if seniors were competitively superior to juniors (Table 1, Fig. 1). Finally, offspring growth was significantly affected by the interaction between the presence or absence of female parents and size rank (Table 1). In the presence of female parents, seniors grew faster than juniors (Fig. 1). In the absence of female parents, seniors and juniors grew at similar rates, although seniors achieved a slightly larger body mass than juniors because seniors continued to grow from the age of 96 h to the age of 120 h, while juniors lost some body mass during the same period (Fig. 1). To verify that seniors grew faster than juniors only in the presence of the female parent, we conducted separate repeated-measures GLMs for the presence and absence of parents, testing for a difference in the growth rate of seniors and juniors from hatching until the age of 96 h. These analyses confirm that seniors grew significantly faster than juniors in the presence of female parents (repeated-measures GLM;  $F_{4,88} = 11.88$ ,  $P < 0.001$ ), but that there was no such significant

difference in the absence of female parents (repeated-measures GLM;  $F_{4,104} = 1.67$ ,  $P = 0.16$ ).

The percentage of offspring surviving to the age of dispersal was significantly higher when female parents were present than when female parents were absent (repeated-measures GLM;  $F_{1,48} = 11.26$ ,  $P = 0.002$ ; Fig. 2). Thus, as predicted, parental care enhanced offspring survivorship. However, there was no significant difference in the survivorship of seniors and juniors (repeated-measures GLM;  $F_{1,48} = 0.34$ ,  $P = 0.56$ ). Likewise, there was no significant effect of the interaction between the presence or absence of parents and size rank on offspring survivorship (repeated-measures GLM;  $F_{1,48} = 0.01$ ,  $P = 0.91$ ). Thus, there was no evidence that the presence or absence of parents had a differential effect on the survivorship of seniors and juniors (Fig. 2).

### Experiment 2: Behavioral interactions

The time that offspring spent feeding from female parents changed significantly with offspring age (Table 2). Offspring increased the time spent feeding from parents between the age of 1 h and the age of 25 h, and then decreased the time spent feeding from parents between the age of 25 h and the age of 49 h (Fig. 3A). There was no significant difference between seniors and juniors with respect to the amount of time feeding from female parents (Table 2, Fig. 3A). Furthermore, there was no significant effect of the interaction between offspring age and size rank (Table 2, Fig. 3A).

The amount of time that offspring spent begging changed significantly as a function of offspring age (Table 2). Offspring increased the amount of time spent begging between the age of 1 h and the age of 25 h, and decreased the amount of time spent begging between the age of 25 h and the age of 49 h (Fig. 3B). Juniors spent significantly more time begging than seniors (Table 2, Fig. 3B). The interaction between offspring age and size rank also had a significant effect on time spent begging

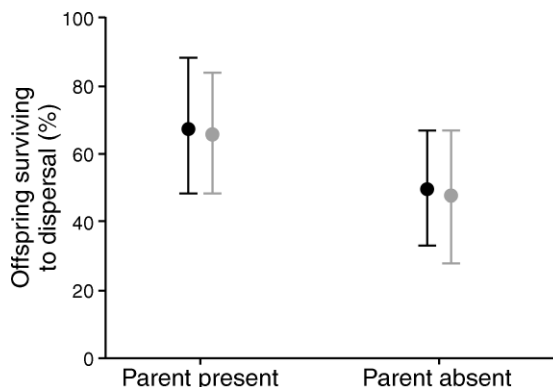


FIG. 2. Effects of the presence or absence of the female parent on the percentage (mean  $\pm$  2 SE) of senior (black circles and lines) and junior (gray circles and lines) *Nicrophorus vespilloides* offspring surviving from hatching until the age of dispersal from the carcass.

(Table 2). This interaction effect occurred because juniors exhibited a greater decrease in the time spent begging between the age of 25 h and 49 h compared to seniors (Fig. 3B).

The offspring's effectiveness of begging (i.e., the return in parental resources for a given amount of begging) changed significantly with offspring age (Table 2). The effectiveness of begging increased between the age of 1 h and 25 h, and then decreased somewhat between the age of 25 h and 49 h (Fig. 3C). Seniors were significantly more effective at begging than juniors (Table 2, Fig. 3C). However, there was no significant effect of the interaction between offspring age and size rank (Table 2, Fig. 3C).

### DISCUSSION

Here we have shown that senior offspring grow faster than junior offspring when begging for resources provided by parents, but that seniors and juniors grow equally fast when self-feeding in the absence of parents. Our findings suggest that asynchronous hatching leads to asymmetric sibling competition when female parents are present and offspring obtain resources by begging, but not when parents are absent and offspring obtain resources solely by self-feeding. Our study extends our knowledge of the ecological significance of asymmetric sibling competition, which until now has been derived almost exclusively from studies on altricial birds. In the burying beetle *Nicrophorus vespilloides*, as in altricial birds, offspring hatch asynchronously and different-aged offspring compete by begging for resources provided by parents. However, unlike altricial birds, offspring are only partially dependent on their parents and parents adjust the brood size directly through filial cannibalism. We will discuss our results in detail in the context of theory for the evolution of parental care and sibling competition.

#### *Experiment 1: Competition in presence and absence of parents*

Offspring grew faster and had a higher survivorship when female parents were present and offspring obtained resources by begging than when female parents were absent and offspring obtained resources solely by self-feeding. This finding is consistent with previous studies examining fitness effects of parental care in *N. vespilloides* and other burying beetles (Eggert et al. 1998, Rauter and Moore 2002, Smiseth et al. 2003b, Lock et al. 2004). These results support a basic prediction from theory for the evolution of parental care: parents provide resources for their offspring because it enhances offspring growth or survival (Clutton-Brock 1991). Furthermore, seniors grew faster than juniors, confirming that asynchronous hatching in *N. vespilloides* (Smiseth et al. 2006) results in competitive asymmetries among siblings, based on hatching order. Similar results have been reported for many altricial birds (Magrath 1990, Stoleson and Beissinger 1995, Mock and Parker

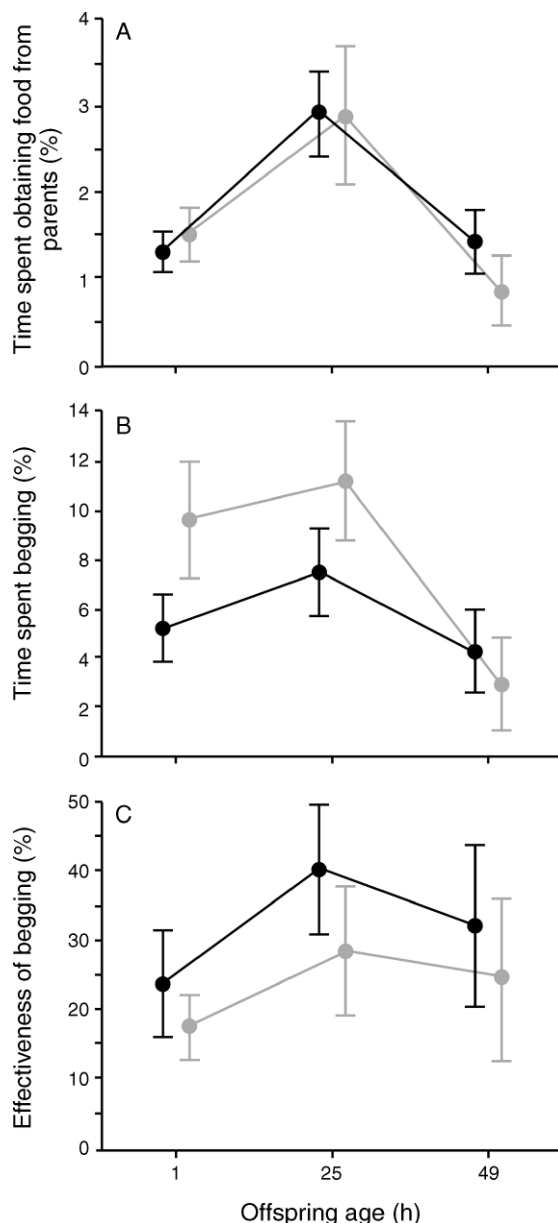


FIG. 3. Behavior of senior (black circles and lines) and junior (gray circles and lines) *Nicrophorus vespilloides* offspring at 24-h intervals during ontogeny starting when the offspring were 1 h of age and ending when the offspring were 49 h of age. Data are presented as means  $\pm 2$  SE. Three behaviors are shown: (A) time spent feeding from the female parent, (B) time spent begging to the female parent, and (C) effectiveness of begging (i.e., the return in parental resources for a given amount of begging).

1997). Finally, there was no difference in the survivorship of seniors and juniors, suggesting that *N. vespilloides* exhibits sublethal forms of sibling competition, such as begging and jostling for position, as found in many passerine birds, rather than lethal forms of sibling competition as found in herons and raptors (Mock and Parker 1997).

The main aim of our first experiment was to examine how parents influence the outcome of asymmetric sibling competition by comparing the growth rate of seniors and juniors in the presence and absence of female parents. We found that the presence or absence of female parents had a differential effect on the growth rate of senior and junior offspring: seniors and juniors grew equally fast in the absence of female parents while seniors grew considerably faster than juniors in the presence of female parents were present. Thus, there was clear evidence that asynchronous hatching led to asymmetric sibling competition when siblings could obtain resources by begging from the parents, but no evidence that asynchronous hatching led to asymmetric sibling competition when siblings foraged independently by self-feeding. A detailed examination of offspring growth in the presence of female parents shows that the growth curves of seniors and juniors began to diverge between the age of 24 h and the age of 48 h and that they were clearly separated by the age of 72 h (Fig. 1). Given that *N. vespilloides* offspring are fully nutritionally independent of their parents by the age of 72 h (Smiseth et al. 2003b), our study shows that the growth curves begin to diverge in the later stages of the period when *N. vespilloides* offspring still depend on resources from their parents.

Thus, we have shown that parental resource provisioning enhances offspring growth, but that it also instigates asymmetric sibling competition. This combined effect is unexpected because theoretical considerations, as well as empirical studies on birds, suggest that asymmetric sibling competition should be associated with limitations in the supply of resources (Drummond and Garcia Chavelas 1989, Mock and Parker 1997, Smiseth et al. 2003a). Given that parental resource provisioning should enhance growth by increasing the offspring's access to limited resources, our surprising result is that parental resource provisioning triggers asymmetric sibling competition despite increasing the offspring's supply of limited resources. Thus, our first experiment provides novel insight into the adaptive consequences of parental resource provisioning, suggesting that further theoretical and empirical work is needed to understand the evolutionary consequences of parental resource provisioning.

#### *Experiment 2: Behavioral interactions*

The main aim of our second experiment was to investigate behavioral interactions among senior offspring, junior offspring, and caring female parents. We found no difference in the overall time that female parents spent feeding seniors and juniors. Thus, in contrast to what we initially expected, there was no evidence that seniors obtained a greater share of the resources provided by female parents than did juniors. However, juniors spent more time begging and were less effective at begging for resources from the parents than were seniors, a pattern also found in asynchronously

hatching birds (Price and Ydenberg 1995, Lotem 1998, Cotton et al. 1999). Studies on *N. vespilloides* and on birds show that junior offspring tend to beg at higher levels than seniors when subject to the same level of food deprivation (Price and Ydenberg 1995, Lotem 1998, Cotton et al. 1999, Smiseth and Moore 2007). Thus, it is unlikely that juniors spent more time begging because they were hungrier than seniors. Our results suggest that senior and junior offspring employ somewhat different begging tactics (Price and Ydenberg 1995, Lotem 1998, Cotton et al. 1999, Smiseth and Moore 2007). Potentially, this divergence could be a consequence of active parental feeding preferences, asymmetries in the competitive abilities of seniors and juniors, or a combination of both. Further research is needed to understand the causal mechanisms underlying the divergence in begging tactics of seniors and juniors.

We found that both time spent feeding from parents and time spent begging increased from the age of 1 h to the age of 24 h, and then decreased from the age of 24 h to the age of 49 h, in accordance with previous studies on *Nicrophorus* beetles (Rauter and Moore 1999, Smiseth et al. 2003b). We also found a difference between seniors and juniors in how their begging effort changed during ontogeny. Juniors spent more time begging than seniors at the age of 1 h and the age of 25 h, whereas juniors spent a similar amount of time begging as seniors at the age of 49 h (Fig. 3B). Thus, juniors exhibited a greater decrease in begging effort from the age of 25 h to the age of 49 h than did seniors. Given that seniors in our design were 24 h older than the juniors, juniors decreased their begging effort at the time when seniors ceased begging, having reached the age of full nutritional independence (Smiseth et al. 2003b). These results suggest that juniors increased their begging effort compared to seniors of the same age when they competed alongside seniors for resources from the parents, but that juniors decreased their begging effort once seniors ceased begging.

#### *How do parents influence asymmetric sibling competition?*

Our experiments show that seniors grow faster than juniors when female parents are present and offspring can obtain resources by begging. To understand the mechanisms by which caring parents influence the outcome of asymmetric sibling competition, we attempt to link the results from our two experiments. One obvious explanation for why seniors grow faster than juniors is that seniors are more successful at obtaining resources than are juniors. However, our first experiment provides no evidence of this explanation, because seniors and juniors grew equally fast in the absence of parents when offspring obtained resources solely by self-feeding. Likewise, our second experiment shows that seniors and juniors spend a similar amount of time feeding from parents, suggesting that seniors are no better than juniors at obtaining resources by begging. Thus, our study



provides no evidence that seniors grew faster because they obtained more resources than did juniors.

Our second experiment shows that juniors spent more time begging than seniors. Thus, juniors might grow more slowly than seniors because they have higher costs of begging than do seniors. For example, in altricial birds, there is evidence that begging incurs an energetic cost, slowing the rate of nestling growth (Kilner 2001). At present, we have no information on the specific costs of begging in *N. vespilloides*. However, offspring begging in *N. vespilloides* might incur energetic costs (as in altricial birds), as well as opportunity costs because offspring cannot self-feed at the same time that they beg for resources from parents. If juniors grow more slowly because they spend more time begging and therefore incur higher costs of begging, the timing for the divergence in growth curves of seniors and juniors should correspond with the time at which there is a difference between seniors and juniors in how begging effort changes as a function of age. Indeed, the growth curves of seniors and juniors diverged between the age of 24 h and the age of 48 h (Fig. 1), which corresponds with the same period when juniors showed a greater change in begging effort as a function of age than did seniors (Fig. 3B). If juniors grew more slowly because they incurred higher costs of begging, juniors should also increase their begging effort relative to seniors during the period when the growth trajectories of seniors and juniors diverge. By contrast, our results show that juniors actually decreased their begging effort relative to seniors during this period (Fig. 3B). Thus, we conclude that there is no support for the suggestion that seniors grow faster than juniors due to differential costs of begging.

Although we cannot pinpoint the exact mechanisms by which seniors grew faster than juniors in the presence of female parents, we have been able to identify the critical period during which the presence of a female parent has a differential effect on the growth of seniors and juniors. We suggest two potential explanations to account for why seniors grew faster than juniors in the presence of female parents. First, the quality or the amount of resources provided by female parents might have changed over time such that seniors were more efficient at converting resources obtained from parents into growth than were juniors. This suggestion could be tested by assessing the quality of predigested carrion provided by parents over time. Second, parents might have affected the offspring's ability to self-feed. This suggestion could be tested by removing parents at various intervals, such as 24, 48, and 72 h after hatching of seniors, and monitoring effects on the growth of seniors and juniors. Thus, further studies are needed to examine the mechanisms by which parental provisioning of resources instigates asymmetric sibling competition.

### Conclusions

The burying beetle *Nicrophorus vespilloides* provides a valuable and interesting model species for advancing our

understanding of how parents influence the outcome of sibling competition. We found that seniors grew faster than juniors in the presence of parents, whereas seniors and juniors grew at similar rates in the absence of parents. However, although parental provisioning of resources may have detrimental effects by instigating asymmetric sibling competition, these effects are countered by the positive effects of parental provisioning of resources on the offspring's growth and survivorship. We encourage further research on the mechanisms by which parental resource provisioning may instigate asymmetric sibling competition, such as potential differences in the quality of resources provided by parents and potential effects of parental resource provisioning on the offspring's ability to self-feed independently of parents.

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